

## EVOLUTION OF THE PERAMELID TARSUS

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**ABSTRACT:** In peramelids, the ectocuneiform bone is incorporated into partial support of the fourth metatarsal, a character unique to that family of Australian marsupials. The incorporation of this bone into support of metatarsal four allows the greater part of the body weight of the animal to pass from the astragalus to the distal tarsals bypassing to a great extent the calcaneum. Such changes in the tarsal arrangement have been influenced by the antecedent development of syndactyly. A similar transfer of body weight, bypassing the calcaneum, occurs in ungulates.

Selected aspects of the hindlimb osteology of peramelids are described and the functional significance of these features is discussed.

## INTRODUCTION

Animals of distant phylogenetic relationships often exhibit similar structural adaptations when subject to similar environmental conditions, i.e. convergence. The tarsal bones of various mammals afford a good example of convergence because of their role in locomotion. They are situated between the pes and lower leg, and transfer the body weight to the foot. Any modifications of the tarsals which channels the vector of weight transfer into a single axial component will inevitably be advantageous to the animal. Animals which progress by similar modes of locomotion should thus exhibit similar adaptations in the tarsal region.

Of the Australian quadruped marsupials, the Peramelidac show modifications of the digits and a tarsal arrangement which converges functionally with those of ungulates. This tarsal arrangement, however, is quite different from that seen in any other groups of similarly adapted animal. In peramelids the ectocuneiform assumes partial support of the fourth metatarsal, while in other animals its function is solely the support of the third metatarsal. This unique arrangement has resulted from the antecedent development of syndactyly.

Bensley (1903) in discussing the foot structures of macropods and peramelids states as a footnote (p. 177) 'The arrangement of the tarsals and metatarsals furnishes a point of distinction. In the Peramelidae the enlarged fourth metatarsal is supported in part by the ectocuneiform and in part by the cuboid, while in the Macropodidae it is practically supported by the cuboid bone'. No

further mention of this 'unique tarsal arrangement' is noted in the literature, nor has the function of such an arrangement been proposed. In this paper selected aspects of the hindlimb osteology of peramelids are described and the functional significance of these features is discussed.

## DESCRIPTION

In order to discuss tarsal modifications and interpret their functional advantage, it is necessary to establish the primitive arrangement of these bones. Figure 1A depicts the tarsal arrangement as it probably occurred in the ancestors of both Eutherian and Metatherian mammals. Among Australian marsupials, *Dasyurus* shows a remarkably similar hind foot structure, identical in fact in the tarsal arrangement, to the generalized Eutherian pes illustrated in Hildebrand (1960, p. 153). For the purpose of this paper I have designated the pes of *Dasyurus* as exhibiting the non-specialized marsupial tarsal arrangement, and as I will show later the specializations in foot structure shown by peramelids, phalangers and macropods may be readily derived from a dasyurid ancestral type.

In the ancestral tarsal arrangement, the astragalus rests essentially on top of the body of the calcaneum with part of the body weight transferred directly to the calcaneum. The articular surfaces of the calcaneum and astragalus with the distal tarsals are nearly equal in area. This indicates a uniform distribution of body weight from the proximal (astragalus and calcaneum) to the distal (navicular, cuboid, and cuneiforms)

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tarsals. All digits are of approximately equal length.

Cursorial quadrupeds inhabiting open flat areas show reduction of lateral digits leading to functional monodactylism, as exemplified by perissodactyls, or didactylism, as occurs in artiodactyls. Associated with digital reduction is an increase in length of the lower leg and foot both absolutely and in relation to the length of the femur (Lull 1904). The contact of the foot with the ground has become restricted to the ends of the digits, which is in contrast to the palmar contact of ancestral stages.

Accompanying these changes, the distal tarsals show greater consolidation either by fusion or elimination of elements. Deepening of the tibial trochlea and associated lengthening of the medial and lateral malleolus along the sides of the astragalus, restricts the foot to anterior-posterior movement.

The astragalus and calcaneum also assume a new relationship. With greater modification in the direction of quadrupedal mono- or didactylism, and greater elevation of the heel from the ground, the body weight is transferred directly from the astragalus to the distal tarsals rather than through the astragalus and calcaneum. The attainment of a quadrilateral shape of the astragalus is associated with these changes.

In perissodactyls (Fig. 1B) this transfer results from an increase in size of the tarsals which function in support of digit three in the ancestral condition. Tarsals not associated with digit three have either fused (entocuneiform and mesocuneiform) or reduced in size (cuboid and calcaneum). In horses the cuboid, although proportionately reduced, is incorporated into support of metatarsal three. Since the astragalus supported digit three via the navicular and ectocuneiform in the ancestral condition, it is these bones which assume support and consequent transfer of body weight.

In artiodactyls (Fig. 1C) the cuboid, ectocuneiform and navicular assume a larger size in response to enlargement of digits three and four while, as a result of digital reduction and functional loss, the entocuneiform is greatly reduced. The mesocuneiform has fused with the ectocuneiform and in the more cursorially specialized artiodactyls (i.e. Pudu, Fig. 1C) the cuboid and navicular are also fused. The cuboid assumes a greater support of the astragalus with consequent crowding of the calcaneum. Any support of the body weight previously attributed to the calcaneum is lost. The astragalus assumes the full role of transfer of body weight to the distal tarsals. Thus, the distal bones of the ungulate tarsus show changes in mechanical relationship associated with

the reduction of digits. The latter is clearly the primary adaptation although tarsal modifications resulting in more direct weight transfer are seen to be closely associated with digital reduction. It is along these lines, digital reduction and a more direct line of weight transfer, that peramelids show a similar adaptation to ungulates.

In peramelids, however, matters have been complicated by the antecedent development of syndactyly in the hind foot. Digits two and three become enclosed in a skin sheath, functioning as a grooming organ; digits one and five are reduced. Digit four is enlarged and assumes total support of the body weight. In the ancestral tarsal arrangement the proximal tarsal contacting digit four (as well as digit five) is the cuboid and this in turn contacts proximally with the calcaneum; thus if the body weight is to be transferred directly to digit four by-passing the calcaneum and paralleling the structural adaptations seen in ungulates, a marked rearrangement of tarsals will have to occur. This is indeed what has happened. In order to document these changes so that they may be followed in a meaningful way, I will first describe the foot structure of *Perameles*, which shows the peramelid modifications in a less developed state, and then *Chaeropus* which exhibits advanced stages in the modifications begun in *Perameles*.

In *Perameles* (Fig. 2A) the entocuneiform is enlarged while the mesocuneiform is reduced and loses contact posteriorly with the navicular. The proximal part of the mesocuneiform is supported partly by the entocuneiform and partly by the ectocuneiform which abut in the area of the original naviculo-mesocuneiform contact. Metatarsal four is supported in part by the cuboid and in part by the ectocuneiform. There is a small flange projecting forward from the medial side of the ectocuneiform supporting the third metatarsal; however, the greater part of the ectocuneiform is incorporated into the support of the fourth metatarsal. In spite of this, the cuboid retains contact with the greatest portion of the fourth metatarsal and all of the fifth metatarsal (Fig. 3A). Accompanying these changes, there is an increase in contact of the astragalus with the navicular. The calcaneo-cuboid contact is reduced in accordance with the reduction of the cuboid.

*Macrotis* exhibits a tarsal arrangement intermediate between *Perameles* and *Chaeropus* (see Fig. 2B). On dental differences, *Macrotis* is less closely related to *Perameles* and *Chaeropus* than the latter are to each other (Bensley 1903). However, the tarsal arrangement seen in *Macrotis* is intermediate between *Perameles* and *Chaeropus* and it is this point with which this study is concerned.



In *Chaeropus* (Fig. 2C) the ectocuneiform-ectocuneiform contact becomes larger and the mesocuneiform is reduced to a mere vestige. The ectocuneiform assumes a greater role in support of metatarsal four. Metatarsal three loses contact with the ectocuneiform and is supported by a syndesmodial articulation in a small groove on the medial side of the fourth metatarsal.

The ectocuneiform has lost its original function (support of metatarsal three) and is incorporated completely into support of the fourth metatarsal (Fig. 3A). The cuboid retains some support of metatarsal four although the area of contact is further reduced. The cuboid retains support of metatarsal five. The astragalo-navicular contact becomes enlarged, the calcaneo-cuboid contact reduced (Fig. 4). The greater part of the body weight is thus directed to the foot via the astragalus. A portion of the body weight is still carried to the calcaneum. However, the calcaneo-cuboid contact is skewed outward at an angle of 30° so that there is potential for slippage and the value of support is reduced. In addition, a posterior encroachment of the navicular occurs on the proximal side of the cuboid, resulting in transfer of weight from the navicular directly to the cuboid. The astragalus assumes a quadrilateral shape although it lacks a deepened tibial trochlea. The presence of a single sole pad near the end of digit four suggests that contact of the foot with the ground is largely restricted to this area.

## DISCUSSION

The changes in tarsal arrangement as exhibited in the series *Perameles*→*Macrotis*→*Chaeropus* has been (1) loss of the mesocuneiform, (2) ectocuneiform shifts role from support of metatarsal three to partial support of metatarsal four, (3) cuboid reduced and shares support of metatarsal four with ectocuneiform, (4) enlargement of astragalo-navicular contact, and (5) reduction of calcaneo-cuboid contact. These changes allow for a great part of the body weight of the animal to be transferred to the distal tarsals, by-passing the calcaneum. Associated with these changes in tarsal rearrangement has been elevation of the heel from the ground, increased allometric growth in metatarsal four in relation to rest of foot, reduction of lateral digits, and restriction of contact of the foot to the anterior end of digit four. The net result has been a functional convergence in the hindlimb mechanics of ungulates and peramelids, with *Chaeropus* exhibiting the ultimate of these specializations in the Peramelidae. It is possible that peramelids were guided by similar selective forces favouring cursorial specializations as occurred in

ungulates (Howell 1944, Lull 1903, Schaeffer 1947).

The hindlimb osteology of peramelids is not totally indicative of a cursorial animal. Jones (1923-25) notes that all peramelids are fossorial in varying degree, although *Macrotis* is the only member that constructs extensive burrows for habitation. Lack of a deepened tibial trochlea and a more rigid contact between the astragalus and calcaneum allows for a great manoeuvrability of the pes which may be associated with this habit. In essence, the structure of the peramelid hindlimb is the result of an evolutionary compromise; the present condition evolving within the limits imposed by the use of the hindlimbs in running and, to a lesser extent, burrowing (by analogy with Vaughan 1970 dealing with a similar concept in bats).

Although the pes of macropods show a close resemblance to the pes of peramelids (i.e. reduction of lateral digits and increase in length of foot as a result of allometric growth in metatarsal four) the tarsals differ considerably in their arrangement (Fig. 3AB, 5ABC). The body weight of macropods is supported to a great extent by the hindlimbs as reflected in the ricochet (bipedal saltation) mode of progression used by these animals, although the front limbs and tail are used in support and movement while the animal is feeding (Frith and Calaby 1969). Consequently the greater the area of contact of the hind feet with the ground, the greater will be the stability of the animal. This is achieved by the hind feet becoming completely plantigrade. The calcaneum increases in size relative to the astragalus as does the astragalo-calcaneal contact. Contact of the astragalus with the distal tarsals is reduced (Fig. 4D). There is no ectocuneiform-metatarsal four contact. The greater part of the body weight is transferred from the astragalus on to the calcaneum, then to the distal tarsals. These changes are in direct contrast to those seen in peramelids (quadrupeds) and are indicative of the different modes of locomotion incorporated by these two groups.

Although both these groups have adapted differently in their modes of progression (peramelids being cursorial quadrupeds and macropods ricochet bipeds) they nevertheless show convergent modifications which are regarded as specializations for speed.

Barnett and Napier (1953) note that . . . 'A further example of convergent evolution within the order marsupialia itself is provided by the development, apparently independently (Bensley 1903) of similar specialized modifications in the fibula of the . . . Macropodidae and Peramelidae

. . . This convergent specialization involves the tibia and fibula being united inferiorly by a syndesmosis that ranges the extent from one-quarter to one-half of the total length of the tibia. They further note that . . . 'The form and mobility of the fibula in these saltatory marsupials is analagous to that occurring in the Eutherians'.

The arrangement of the tarsal bones in peramelids and macropods is readily derived from that arrangement shown in phalangerids (Fig. 4B). Peramelids have deviated from the phalangerid condition in the relationship between the cuboid, ectocuneiform, and metatarsal four as discussed earlier. The calcaneum, astragalus and navicular arrangement is essentially unaltered although the contact between the astragalus and navicular becomes larger in the peramelids while the calcaneo-astragalus contact shows relative reduction. *Perameles* exhibits a late stage in this transformation with the ectocuneiform supporting both metatarsal three and four. Both groups are syndactylous. Macropods have deviated from the phalangerid condition in the relationship between the astragalus, navicular, and calcaneum. In macropods the astragalo-calcaneum contact is greatly enlarged while the astragalo-navicular contact is greatly reduced. There has been no change in the relationship between the cuboid, ectocuneiform and metatarsal four as is seen in peramelids. Macropods are also syndactylous. In peramelids, the net result of these changes has resulted in the channelling of the greater part of the body weight along a vector as shown in Fig. 6A; while in macropods the greater part of the body weight passes in a vector as shown in Fig. 6B. The phalangerid tarsal arrangement allows the body weight to be more evenly distributed on to the foot by utilizing both these vectors more equally; the resulting transfer of body weight being directed as shown in Fig. 6C.

The changes exhibited in the macropods and peramelids are the result of the utilization of the fourth digit as the main support digit. The resulting difference between peramelids and macropods, utilizing different vectors of transfer of body weight to digit four, are linked with the quadrupedal mode of progression of peramelids and a bipedal mode of progression of macropods. The result has been a more direct vector for weight transfer on to the main supporting surface of digit four. In peramelids the weight is directed toward the most distal end of digit four, in macropods it is directed more toward the heel.

The derivability of the peramelid and macropod tarsal arrangement from the phalangerid tarsal arrangement suggests that syndactyly need have arisen only once in the Australian marsupials as

opposed to a double origin as proposed by Tate (1948, p. 317). As the peramelid and macropod foot structures are both derivable from a phalangerid type foot it may be concluded that the tarsal-metatarsal arrangement shown in phalangerids is the primitive arrangement and was that arrangement which occurred in the ancestors of these two groups. By further extrapolation it is seen that as the tarsal-metatarsal arrangement is identical in dasyurids and phalangerids, the loss of syndactyly in phalangerids (digits two and three becoming separated) would result in a foot structure identical to that of dasyurids (Fig. 4A). The dasyurids thus show a foot structure from which all modifications occurring in the present-day Australian marsupials could have been derived.

Tarsal bones are also important as basic indicators of various taxonomic ranks. The evolution of the tarsus and subsequent calcaneal alterations have resulted in the introduction of basic ordinal characters in artiodactyls (Schaeffer 1947) and perissodactyls (Radinsky 1966). Robinette and Stains (1970) have shown that a study of the calcanea of pinnipeds may give some indication of the relationships among members of the different families and possibly some indication of ancestry. Similar results establishing the importance of tarsal bones in taxonomy have been reported by Stains (1959, 1962) and Romankowowa (1963). Although most of these workers have based taxonomic importance on the astragalus and calcaneum, there is little reason why a gross rearrangement of the distal tarsals should not receive a similar consideration. Of the Australian marsupials, the ectocuneiform-metatarsal four contact is a unique morphological entity found only in the peramelids (Gregory 1951, Fig. 18, 20 has erroneously shown the wombat with an ectocuneiform-metatarsal four contact).

Of the Australian marsupials, the Peramelidae are polyprotodont and syndactylous while all other Australian polyprotodonts are didactylous and the diprotodonts are syndactylous (see Jones 1923-25, Ride 1964, Tate 1948). The presence of both polyprotodonty and syndactyly in peramelids has caused considerable difficulties in the higher taxonomic position of this group (see Ride 1962, 1964). Perhaps the ectocuneiform-metatarsal four contact is the diagnostic character which truly sets peramelids apart from their contemporary relatives, and that such a difference may warrant taxonomic consideration.

## SUMMARY

In peramelids the greater part of the body weight is transferred to the foot via a vector passing from the tibia-astragalus-navicular-ectocunei-



form-metatarsal four. This has resulted in an alteration in the relationships between the cuboid, ectocuneiform and metatarsal four from that arrangement of these bones seen in the foot structure of a proposed phalangerid ancestor. This vector of transfer of body weight is linked with a quadrupedal mode of locomotion. The resultant ectocuneiform-metatarsal four contact is unique to the Peramelidae among the Australian marsupials; it has been suggested that such differences may warrant taxonomic consideration. Ungulates exhibit similar modifications regarding weight transfer and the result has been a functional convergence in the hindlimb mechanics between these two groups.

In macropods the greater part of the body weight is transferred to the foot in a vector via the tibia-astragalus-calcaneum-cuboid-metatarsal four. This vector of weight transfer is linked with a ricochetal (bipedal saltation) mode of locomotion. The main alterations from an ancestral phalangerid tarsal arrangement are seen in the relationship between the astragalus, navicular, and calcaneum.

The various changes in weight transfer as seen in macropods and peramelids have resulted from the antecedent development of syndactyly of digits two and three on the hind foot with digit four becoming the main supporting digit. In Eutherians, perissodactyls utilize digit three as the main support digit and in artiodactyls it is digits three and four. In peramelids, tarsal rearrangement was necessary before the body weight could pass to the distal tarsals, by-passing to a great extent the calcaneum as does occur in ungulates.

As the peramelid and macropod foot structures are both derivable from a phalangerid foot structure, it is suggested that syndactyly need have arisen only once in the Australian marsupials. The acquisition of syndactyly in dasyurids would result in a foot structure identical to a phalangerid foot, save for relative differences in digit size. It is thus proposed that the foot structure as seen in dasyurids may have been that condition seen in the ancestors of all Australian marsupials. The evolution of the various modifications in foot structure in Australian marsupials has probably progressed in a line from dasyurids to phalangerids, with the latter branching and giving rise independently to peramelids and macropods (see Fig. 4 of this paper; and Goodrich 1935, p. 177).

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## EXPLANATION OF TEXT-FIGURES 1-6

- FIG. 1—Mammalian pes (right). A, hypothetical mammalian ancestor; B, horse (Perissodactyl); and C, Pudu (Artiodactyl): modified from Hildebrand, 1960. Abbreviations: cal, calcaneum; mc, mesocuneiform; as, astragalus; cu, cuboid; ec, ectocuneiform; en, entocuneiform; nav, navicular; digits I, II III, IV V.
- FIG. 2—Pes of peramelids (right). A, *Perameles*; B, *Macrotis*; and C, *Chaeropus*. Note that associated reduction of digits I, II, III and V is accompanied by elongation of digit IV, largely the result of allometric growth in metatarsal IV. For abbreviations see Fig. 1.
- FIG. 3—Proximal end of right metatarsals of A, *Macrotis* and B, *Macropus* showing contact surfaces with tarsals. Note the large contact area of the ectocuneiform with metatarsal IV in *Macrotis*. In *Macropus* metatarsal IV contacts only with the cuboid. For abbreviations see Fig. 1.
- FIG. 4—Dorsal view of tarsals (astragalus removed) showing contact of astragalus with calcaneum and navicular (vertical hatch). The illustrations: A, dasyurid (*Dasyurus*); B, phalangerid (*Trichosurus*); C, peramelid (*Perameles*); and D, macropod (*Macropus*) are arranged diagrammatically in probable order of derivation. A and B are similar with regard to tarsal arrangement as well as showing a similar division of contact of the astragalus between the calcaneum and navicular. Note that in C (*Perameles*) the contact of the astragalus with the navicular is large while in D (*Macropus*) this contact is small while the contact of the astragalus with the calcaneum is greater in D (*Macropus*) and smaller in C (*Perameles*). These differences represent extremes which have deviated greatly from the more even distribution of these contacts (astragalus-navicular, astragalus-calcaneum) as seen in B (*Trichosurus*). Note encroachment of navicular on to proximal end of the cuboid in C (*Perameles*).
- FIG. 5—Pes of macropods (right). A, *Thylogale*; B, *Macropus*; and C, *Megaleia*. For abbreviations see Fig. 1.
- FIG. 6—Diagrammatic representation showing the force vector along which the body weight is transferred to the supporting digit(s) in A, peramelids; B, macropods; and C, phalangerids. For explanation see text.

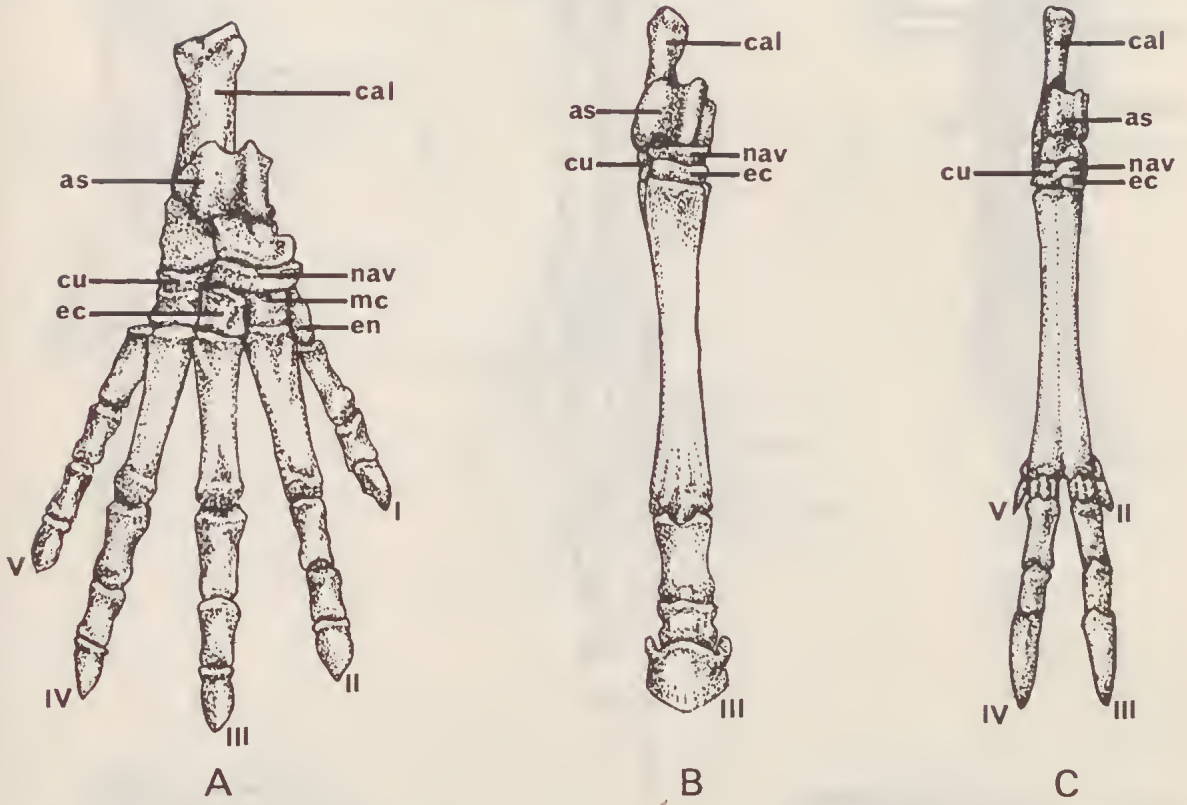


FIG. 1

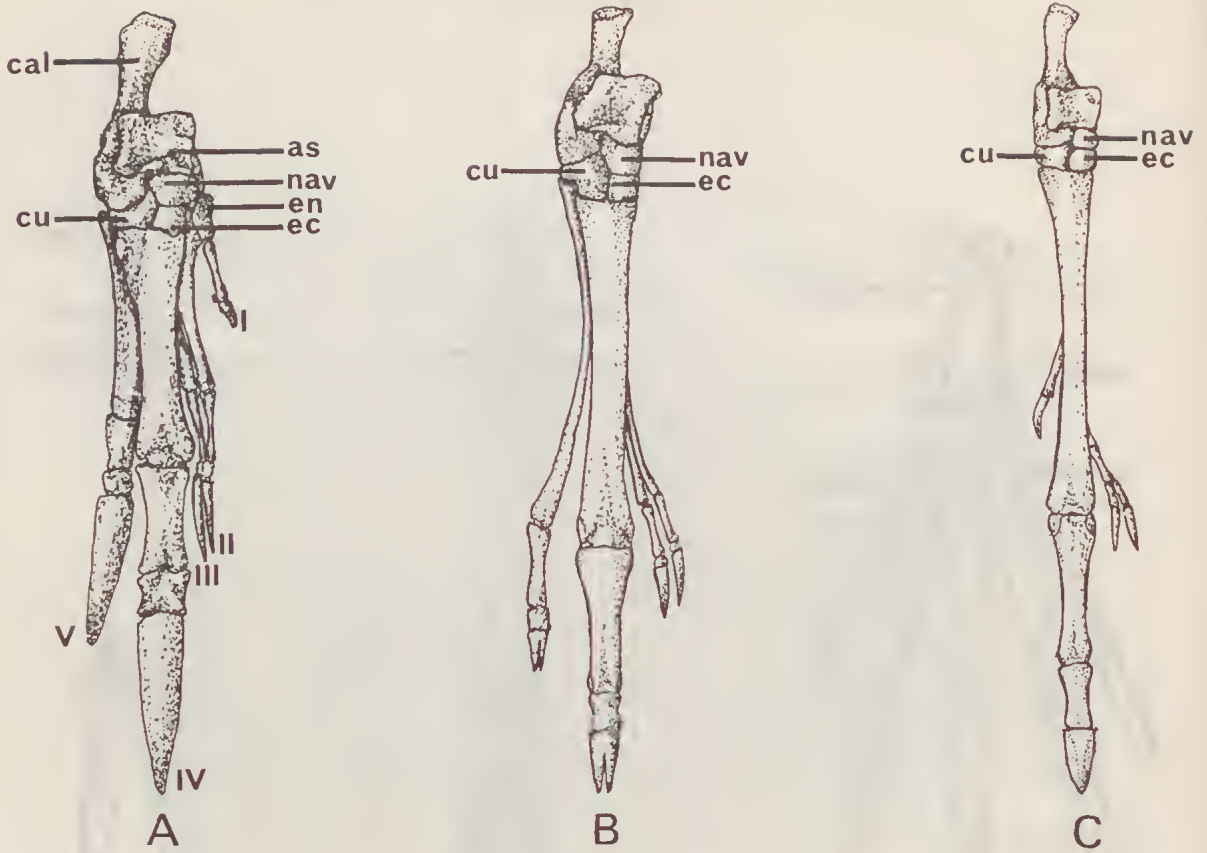
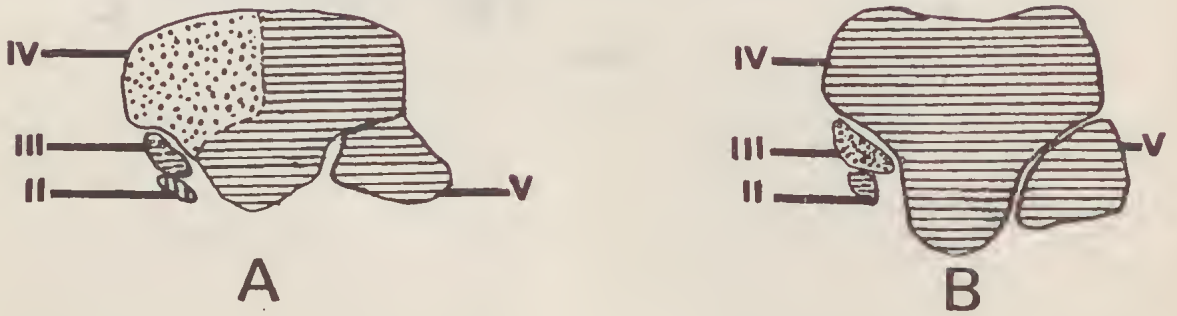


FIG. 2



- |   |   |
|---|---|
|  ectocuneiform |  cuboid        |
|  entocuneiform |  mesocuneiform |

FIG. 3



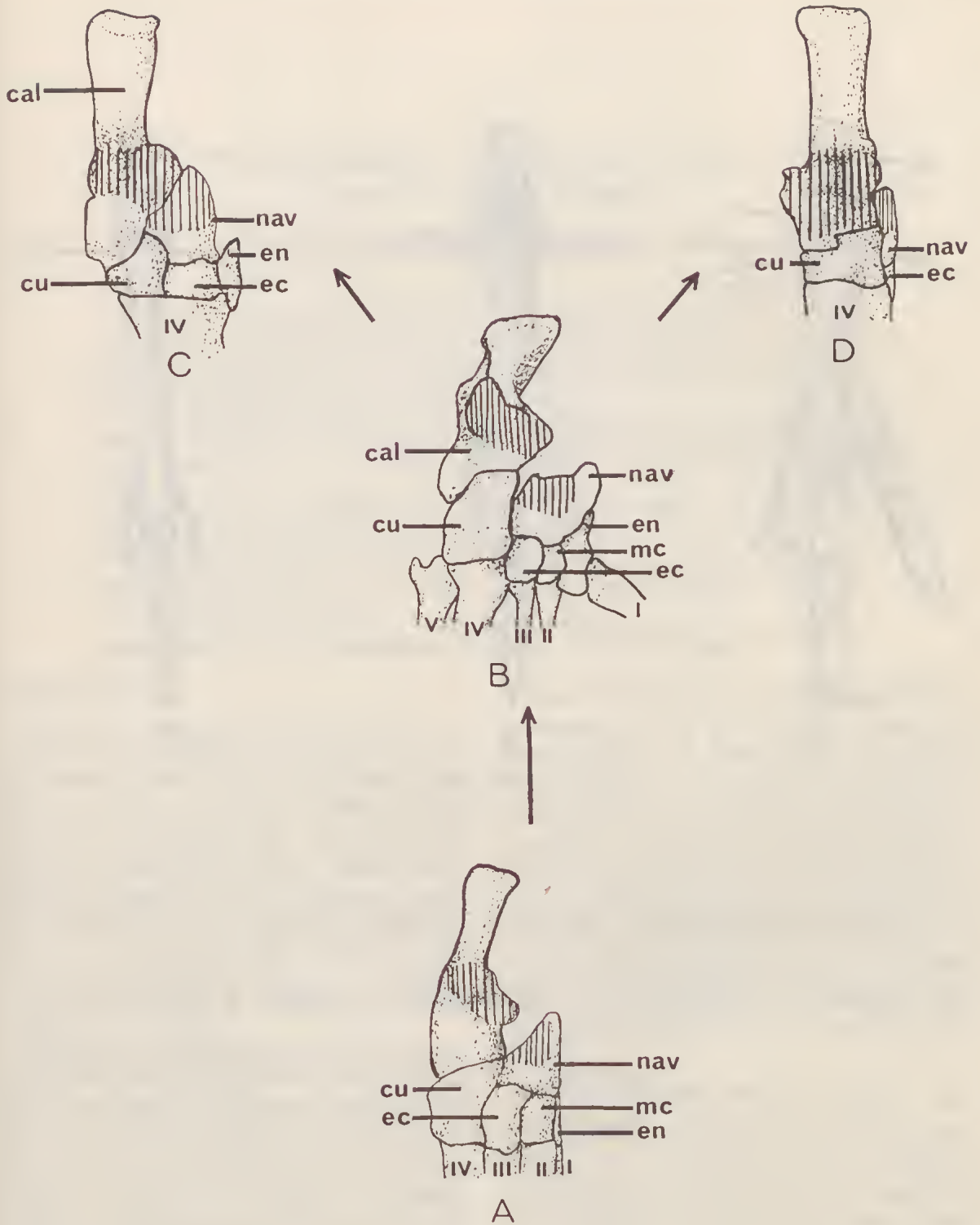


FIG. 4

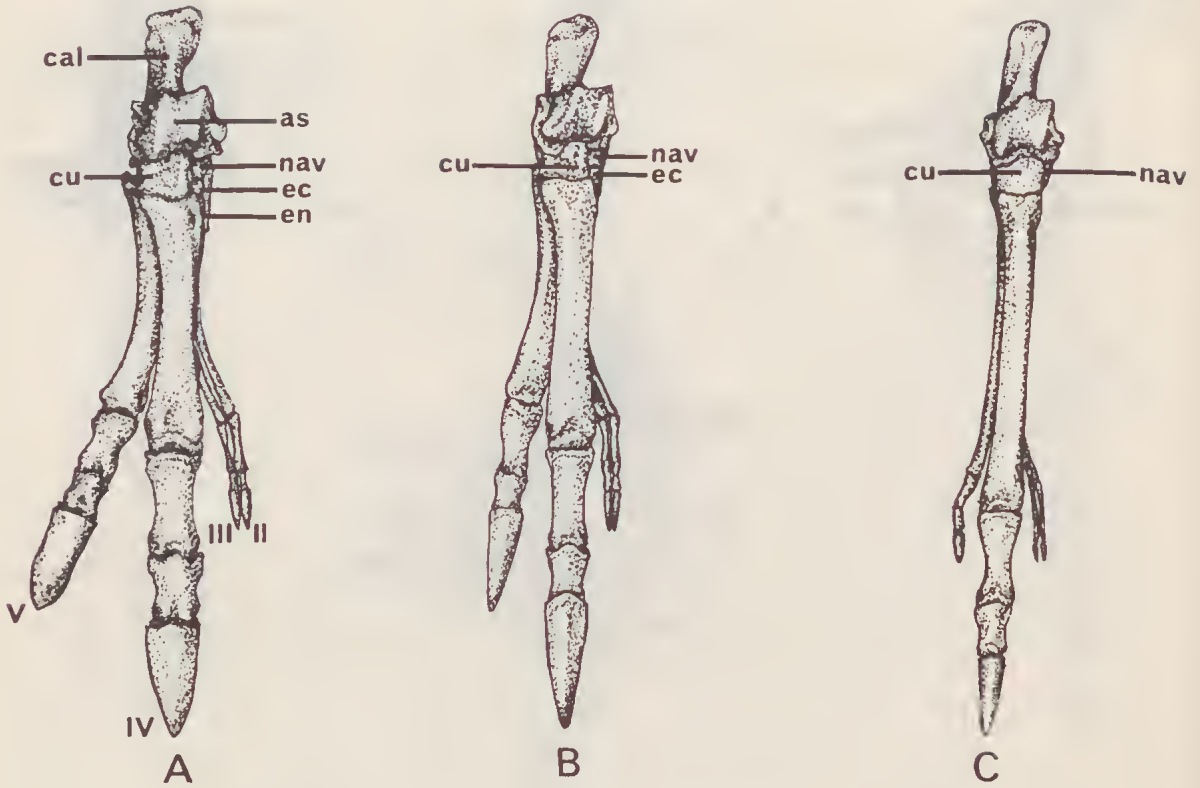


FIG. 5

- A. tibia → astragalus → navicular → ectocuneiform → metatarsal IV
- B. tibia → astragalus → calcaneum → cuboid → metatarsal IV
- C. tibia → astragalus → <sup>navicular</sup> → cuneiforms → metatarsals I, II, III  
<sup>calcaneum</sup> → cuboid → metatarsals IV, V

FIG. 6